Molecular relationships in the seaweed genus Cladophora

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SUMMARY

One topic common to all biogeographic research is change over space and through time. Ecologists, studying the relationships between organisms and their environment, are concerned with spatial change. Historical biogeography deals with relationships between the earth's history and the distribution of organisms, thus, with change through time. In the present state of knowledge it is difficult to come to integrated hypotheses concerning the historical causes of seaweed distribution patterns. An important reason for this is the lack of information on relationships between geographically distant seaweed populations and seaweed species.

A lack of sufficient information on relationships is certainly true for the green algae genus *Cladophora*. A number of species of this genus are distributed world-wide, but the history and the factors that caused this distribution are not or poorly known. Furthermore, most *Cladophora* species are notoriously variable with respect to their morphology, a factor that complicates the formulation of unequivocal taxonomical conclusions.

The aim of this thesis was to address the role of historical biogeographic factors on the distribution patterns of some *Cladophora* species, by considering the geographic distribution of inter- and intraspecific DNA divergence. The primary strength of this method is that it yields data directly in the form of distances which in turn can be used in biogeographic analyses.

The resemblance, at least with regard to the amount of repeated DNA sequences, between the nuclear genomes *Cladophora* species and the genome of an average higher plant is one of the results presented in chapter 2. The chapter further presents data which indicate that the high level of DNA similarity between East and West Atlantic isolates of *C. sericea* is the result of trans-Atlantic dispersal which presumably took place after the last glaciation.

C. albida is distributed in the warm to warm temperate climatic belts of the northern and southern hemispheres. North Atlantic and Indo-West Pacific isolates of this species differed to such a degree when analyzed for their DNA that they can be classified as morphologically indistinguishable, but different species. The correlation between the observed DNA divergence and the present distribution of the isolates tested raised the suggestion that *C. albida* had been divided into a North Atlantic and an Indo-West Pacific group as a consequence of an allopatric subdivision. It is assumed in chapter 3 that this subdivision could have been initiated by the Miocene closure of the Asian part of the Tethys ocean. Support for this vicariant mode of speciation came from DNA hybridizations between species of the *C. pellucida* group (chapter 4). This subgroup in the genus *Cladophora* is comprised of stenothermous species with relatively restricted distribution areas. DNA hybridizations between North Atlantic and Australian

species of this group showed the same overall picture as had been observed in *C. albida*. Moreover, the divergence between two other species of the *C. pellucida* group, endemic to the East and West Atlantic coasts, could also be related to a Miocene event, namely to the steepening of the latitudinal temperature gradient along the West Atlantic coast. This congruence between the geographic patterning of DNA divergence in two hardly related *Cladophora* groups and the areas of the present distribution of their species suggests that a common set of historical biogeographical factors may have accounted for these patterns, and that for these species dispersal has not overridden these factors.

Above vicariance mode of speciation does apparently not hold for *Cladophora* species distributed in both the warm temperate and the tropical sector of the Atlantic ocean. DNA of North Atlantic and Australian isolates of species that exhibit this distribution type (*C. vagabunda* and *C. laetevirens*) was relatively moderately diverged (chapter 5). This suggests that the broad temperature tolerance range of these species permits dispersal through the topics. At the same time, it is an indication that the tropical sector, of at least the Atlantic ocean, forms an obstacle for the North-South dispersal of warm temperate species such as *C. albida* and *C. pellucida*.

The existing taxonomy of the genus *Cladophora*, build on a purely morphological basis, is only partially supported by DNA hybridization data (chapter 6). The low NPH values observed between formsections in the genus do not exclude the possibility that the morphological trends which characterize these sections represent an early phylogenetic radiation. On the other hand, the, on the whole, low NPH values between species and, in some cases, between conspecific geographic isolates, indicate that *Cladophora* species may comprise complexes of "real species" which hardly can be distinguished with the aid of the morphotaxonomical characters presently in use.

The correlation between the two data sets produced by the DNA hybridization method used in this thesis (the reduction of the initial degree of hybrid formation and thermostability lowering of hybridized sequences) differs between very different groups of organisms. This difference is probably only the tip of the genome evolutionary iceberg underlying DNA hybridization data. But the major issue of chapter 7 is that differences in the internal strategy of genomic evolution affect the robustedness of DNA hybridization data, a factor which raises questions with respect to the utility of these data as indicators of time dependent DNA evolution.

The relation between the data of DNA hybridization and genomic evolution is further extended in chapter 8 in which isozyme banding patterns are compared with DNA hybridization data. The, although preliminary, conclusions are that the minimum estimates of realized num-

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bers of nucleotide substitutions in sequences that code for a specific function increase at reduced DNA homology levels. This means that DNA evolution as indicated by DNA hybridizations is not linear, but curvilinear related to evolutionary time elapsed. In other words the greater the time of separation between organisms the slower the rate of DNA evolution appears to be.

The discussion in chapter 9 tries to explain the general trend in the North Atlantic of an increasing number of East and West Atlantic endemics as one approaches the tropics. Analyses of DNA hybridizations between amphi-Atlantic *Cladophora* isolates suggest that, at least for the species tested, the North Atlantic ocean does not act as an absolute dispersal barrier, but that present and historical ecological factors at the end points of this barrier (the Atlantic coasts) were and, probably are, decisive in this respect.